Analysis of litter size in a colony of the common marmoset *(Callithrix jacchus)*

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Abstract

In our *C. jacchus* colony the incidence of triplet litters is slightly higher than that of twin births. The observation of litter size incidence as an annual event, as has been done in the literature masks important details of litter size distribution. The wild-caught females of our colony gave birth to nearly twice as many twins than triplets, and we could not recognize a tendency to produce more triplets in conjunction with increasing length of captivity in our laboratory. The most conspicuous changes in the relative frequencies of litter size compared to wild-caught females occurred in the F_1-generation. The relative frequency of quadruplets and triplets increased enormously, whereas that of twins and singletons decreased considerably. In the following generations (F_2 to F_4) we observed again a definite increase in twin sets, with an associated decrease in triplet sets. Therefore the often repeated statement, that a refined management will lead to an increase of triplet deliveries, apparently is neither sufficient nor correct.

Introduction

As a rule marmoset females are multiparous (survey of the literature see Rothe 1979). However, this observation originates from laboratory kept colonies, whereas very little information on this aspect in free ranging marmoset populations is available (e.g. Hubrecht 1984).

Many marmoset colonies which are kept and bred under laboratory conditions, show an increase of triplet births, a phenomenon which has been considered by some authors to be due to the generally better living conditions, i.e. nutrition, medical care etc., of primates in captivity than would be possibly true for free living individuals (see for example Hiddleston 1978). Kirkwood et al. (1983) observed a sudden and enormous increase of triplet births in *Saguinus oedipus* after the authors had reduced the ratio of carbohydrates in favour of protein in the daily diet. However, we do not know as yet whether the increase of triplet births in captive marmosets results from an augmentation of the ovulation rate or from a reduction of the prenatal death rate of ova/zygotes. From other animal species, on the contrary, we have better information on this aspect. Voss (1950, 1952) (sheep), Lüdike-Spannenkrebs (1955) (rabbit), and Boye (1956) (pig) observed an intensified follicular activity and an increased production of ova in captive individuals in comparison with their respective wild counterparts. Moreover, with some domestic animals and some wild species, e.g. *Clethrionomys glareolus* (Brambell 1948) a reduced prenatal mortality of ova/zygotes could be detected under laboratory conditions (see also Schilling 1952; Michaelis 1966; Sadleir 1969); and, according to Boye (1956) some uterine conditions, for example, size, weight, vascularisation, seem to have a considerable effect on fetal mortality.

To what extent the genetical constitution of the marmoset females plays a role on the disposition to produce more triplets/quadruplets with increasing age, remains to be

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investigated. From human females for example we know, that the age of the mother and the parity are important factors associated with the occurrence of dizygote twins/triplets (Vogel and Motulsky 1979).

Material and methods

202 litters of the common marmoset, including five abortions (definition see König et al., in press) from 44 breeding females of our colony which has been in existence since 1968, were analysed. Eight females were wildcaught (wc), 15 F_1-, 15 F_2-, 4 F_3- and 2 F_4-generation (Table 1). 8 of the 44 females are still living and breeding in our laboratory. Further details on the animals are shown in Table 1.

Results

46.04 % (n=93) of all identifiable litters (n=202) of our colony of common marmosets were triplets (Tr); twin (Tw) births occurred 80 times (=39.6 %); singletons (Si) 18 times (8.94 %), and quadruplets (Qu) 11 times (=5.45 %). Abortions and premature births occurred in 5.94 % (n=12) of the births, whereby in 7 cases the size of the respective litter could not be identified, the remaining five consisted of one triplet, two twins, and two singletons. No less than three abortions occurred in one female (F45, Gr. F, Table 2).

A break down of the data on litter size according to the females' generation shows the following results. The wild-caught females (n= 8, 53 litters) had fewer triplets (n=16, 30.19 %) than twins (n=30, 56.60 %). Quadruplets occurred only once (F15, Gr. A1). Quite different results come from the F_1-females (n=15, 83 litters). The percentage of quadruplet births amounted to 9.64 (n=8), of triplets to 61.45 (n=51), whereas twin deliveries were clearly in the minority (n=18, 21.69 %). Only slight differences are apparent between the relative frequency of singletons of wild-caught and F_1 females (wcF: 11,32 %, n=6; F_1F: 7.23 %, n=6). The females of the F_2-generation (n=15, 36 litters) differ widely from the F_1-females as to litter size distribution. They had only 47.22 % (n=17) triplets, whereas the percentage of twin births was 44.44 (n=16). In the F_3-generation the frequency of triplets dropped down to 26.9 % (n=7), and the percentage of twin births increased to 56.69 (n=15). The F_3-females have a relatively high frequency of singletons (=15.38 %, n=4). It must be stressed however, that in relation to the number of females, the number of litters is substantially lower in the F_2-generation than in the F_1-generation. For that reason we cannot decide wether the striking differences in the percentage of the different litter sizes are characteristic for F_2-females or are artifacts arising from the differences in the number of litters of the two generations. The same restriction is true for the F_3-females (n=4), although, all things considered, we have observed a strong tendency to have twin births. From the F_4-females we have had only four deliveries up to now from two females, so that we cannot as yet comment on the distribution of litter size in that generation.

The compilation of the data according to consanguinity of the breeding females of our colony reveals some more interesting results (Table 4). The most conspicuous, of which, is the familial accumulation of quadruplets. No less than six (=54.54 %) of the eleven quadruplet sets occurring since 1968 were observed in four F_1-sisters, daughters of one wc-founder female (F12, Gr. B, Table 1) of our marmoset population. If one includes a great-great-grand-daughter of F12, 63.63 % (n=7) of all quadruplets we have had hitherto, have occurred in clan B. Three Qus were born in clan CJ, two by the mother and one by one of her daughters (Table 4). That is, more than 90 % of Qus of our *C. jacchus* females are restricted to two clans. Only one female (F15, wc, Table 1) which had Qus was not related to the other Qu-mothers.

The direct comparison of the litter size of clan-mothers and of their respective

Table 1. **Survey of all groups and breeding females**

Group	No. of female	Generation	Number of litter 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Comments
A1	0015	wc	4	2																			
B	0012	wc	3	3	2	2	2	2	2	3	3	3	2	1	3A								
C	0011	wc	?A	2	2	2	2	1	3	3	3	3	1	3	3	2	3	3	2	2	3	1	a
D	0004	wc	2	2	2	2	2	2	2														
E1	0014	wc	2A	3																			
CO	0441	wc	2	1	2	2																	
CP	0439	wc	2	2	2																		
CQ	0440	wc	1	2	2																		
C′	0052	F1	3	2	2A																		b
F	0045	F1	3	1	3	1	A	A	4	3	3	4	3	A									c
G	0032	F1	3	3	3																		
I	0049	F1	3	3	3	2	3																
J	0060	F1	3	2	1	4	3	3	4	2	2												
K	0059	F1	3	A	2	3	3	2	3	2													d
L	0054	F1	3	3	3	4	3	2															
M	0051	F1	3	2	3	3	3																
N	0053	F1	2	3	1	4	3																e
R	0068	F1	3	3	3	2	3	3															
S	0038	F1	2	3	3	3																	
CE	0302	F1	1	3	3	3	2	3	3	3	3												f
CJ	0349	F1	3	3	3	3	4	4	3	2													g
CK	0357	F1	1																				h
CL	0356	F1	2	2	3																		i
M	0136	F2	3	2																			j
U	0257	F2	3																				k
V	0123	F2	2	3	3	2	2																l
X	0245	F2	3	3																			
Z	0215	F2	2																				
NN	0155	F2	2																				
CB	0166	F2	2	2	2	2	2																
CC	0143	F2	3	3	3	3	A																
C″	0231	F2	2	2																			m
CF	0341	F2	1																				n
CI	0251	F2	2	3	3	1	3	3															
CN	0383	F2	3																				
CU	0384	F2	3	3																			
CV	0410	F2	4																				
CD	0269	F3	1A	2	3	3	2	2	2	2	3	3	3	1									
CG	0270	F3	A	3	1																		
CH	0313	F3	2	2	2	2	2	2	1A														
CM	0334	F3	2	2	2	3	2																
CS	0365	F4	3	2	3																		
CT	0403	F4	4																				

a: following birth of litter 20, group was dissolved, female 0011 received another male companion
b: brother and sister were breeding
c: father died shortly after birth of litter 4, from then on the eldest son bred with the mother
d: after birth of litter 8, alpha female was paired with a new male
e: male partner of female 0076 was only 9.5 months when paired unintentionally
f: female 0302 was presumably F1-generation
g: litter 8 were presumably twins
h: female 0357 died due to complications during birth of litter 1
i: female 0356 was often in poor condition
j: father and daughter were breeding
k: female 0257 had been hand reared
l: female 0123 was already pregnant when paired
m: female 0231 was only 28 months old when litter 1 was born
n: brother and sister were breeding
wc = wildcaught; A = abortion; ? = litter size not identifiable; 1 = singleton; 2 = twins; 3 = triplets; 4 = quadruplets

Table 2

Frequency of quadruplets, triplets, twins, singletons, and abortions

	Quadruplets	Triplets	Twins	Singletons	Σ/%
absolute frequency	11	93	80	18	202
relative frequency	5.45	46.04	39.60	8.91	100
abortions no. of fetuses identifiable	–	1	2	2	5
abortions no. of fetuses not identifiable					7
relative frequency of abortions					5.94

daughters reveals the following results. F12, mother of clan B, had 13 litters with a balanced relation of Tr- and Tw-deliveries (n=6 each, 46.15 %). This female had only one Si. Her five daughters on the contrary mainly had Trs (n=21, 53.85 %) and Qus (n=6, 15.37 %), but relatively few Tws (n=8, 20.51 %). Only slight differences exist in the frequency of Sis of the mother (= 7.69 %) and her daughters (=10.26 %). If one compares the size of the litters of the clan-mother with those of all breeding females which are related to her, only minor differences can be observed in the frequency of Trs (46.15 % and 47.5 %); and the differences in the portion of Tws also is reduced. That is to say, mother and daughters have more differences when one compares the size of their litters, than the mother and the group of all her breeding female descendants.

Clan mother F11 (Gr. C) has nearly as many Trs (=47.32 %) as F12. F11 has relatively fewer Tw-deliveries (n=7, 36.84 %) and more Sis (n=3, 15.79 %). Her daughters showed remarkable differences to their mother in the distribution of litter size: 16 Tws, (26.09 %); 17 Trs (73.91 %). Sis were not born. In clan C too, with the exception of the relative frequency of Sis (n=4, 6.56 %), the group of all female descendants of the clan mother F11 does not deviate so far the litter size distribution of the founder female as does the group of her daughters. Litter size distribution in clan C shows greater differences from the distribution of the total population of breeding females of our *C. jacchus* colony than holds true for clan B.

Female F269 (clan CD) resembles in the litter size distribution her great-grand-mother (F12, clan B), except for the frequency of singletons (n=2, 16.67 %). Also in this group of related females the daughters deviate more strongly from the litter size distribution of their mother than does the group of all female descendants from their founder female F269. Except of slight differences in the litter size distribution, clan CD reflects nearly exactly the colony distribution.

Founder female F59, clan K, daughter of F12, shows an equal frequency of Tr- and Tw-births (n=4, 57.14 % rsp. n=3, 42.86 %), with the daughters resembling their mother in this respect. However, the number of litters is very low (n=5).

Clan V (F123) shows a nearly identical distribution of litter size with that of clan mother F269 (Gr. CD), a daughter of F123. As a whole, both clans differ mainly only in the frequency of Qus. In the other three clans (CE, F302; CJ, F349; CL, F356) the number of litters is too low to be described separately (see Table 4).

The analyse of litter size according to parity reveals following results. The wc-females (n=8) predominantly have Tws (n=45) even when they have lived for many years in captivity. At first one can observe an increase of Tw-deliveries to the disadvantage of Trs and Sis. In the F_1-generation we detected a great spread of the different litter sizes along the sequence of deliveries (15 females, 82 litters). The Trs dominate from the start of the sequence, but there is no further increase of Trs with increasing parity whereas this is true for Qus, mainly to the detriment of Sis and Tws. Also in the F_2-generation (15 females, 35 litters) we did not observe a continuous increase of Trs in relation to parity but instead a

Table 3

Absolute and relative frequency of litter size in relation to the females' generation

Generation/	N Females	N Deliveries	N Litters	N Abortions		Quadruplets		Triplets		Twins		Singletons	
				ni	i	N	%	N	%	N	%	N	%
wc	8	54	53	1	1Tr,	1	1.9	16	30.2	30	56.6	6	11.32
F1	15	87	83	4	1Tw	8	9.64	51	61.45	18	21.7	6	7.23
F2	15	37	36	1	1Tw	1	2.78	17	47.22	16	44.44	2	5.56
F3	4	27	26	1	–	–	–	7	26.92	15	57.7	4	15.38
F4	2	4	4	–	2S	1	25.0	2	50.0	1	25.0	–	
					–								
Σ	44	209	202			11	5.45	93	46.04	80	39.60	18	8.91

ni = litter size is not identifiable; i = litter size is identifiable. N = absolute number; wc = wildcaught; Tr = triplets; Tw = twins

Table 4

Absolute and relative frequency of litter size in related females

Clan		B				C				V				CD				CE				CL				CJ			
Litter-size		Q	Tr	Tw	S	Q	Tr	Tw	S	Q	Tr	Tw	S	Q	Tr	Tw	S	Q	Tr	Tw	S	Q	Tr	Tw	S	Q	Tr	Tw	S
I	n	–	6	6	1	–	9	7	3	–	2	3	–	–	5	5	2	–	7	1	1	–	1	2	–	2	5	1	–
	%		46.2	46.2	7.7		47.4	36.8	15.8		40.0	60.0			41.7	41.7	16.7		77.8	11.1	11.1		33.3	66.7		25.0	62.5	12.5	
II	n	6	21	8	4	–	17	6	–	–	6	5	3	1	2	1	–	–	3	–	–	–	–	2	–	1	–	–	–
	%	15.4	53.9	20.5	10.3		73.9	26.1			42.9	35.7	21.4	25	50	25			100					100		100			
	N		6				5				2				2				2				1				1		
III	n	7	38	26	9	–	23	18	1																				
	%	8.8	47.5	32.5	11.3		54.8	42.9	2.4																				
	N		18				10																						
IV	n	6	27	14	5	–	26	13	3	–	8	8	3	1	7	6	2	–	10	1	1	–	1	4	–	3	5	1	–
	%	11.5	51.9	26.9	9.6		61.9	31.0	7.1		42.1	42.1	15.8	6.3	43.8	37.5	12.5		83.3	8.3	8.3		20.0	80.0		33.3	55.6	11.1	
V	n	7	44	32	10	–	32	25	4																				
	%	7.5	47.3	34.4	10.8		52.5	41.0	6.6																				

Q = quadruplets; Tr = triplets; Tw = twins; S = singletons. I = clan mother; II = daughters of clan mother; III = all breeding descendant females of clan mother; IV = clan mother and daughters; V = clan mother and all breeding descendant females.

Table 5

Number of groups and females; generation; number of litters and litter size

Group	No. of female	Natal Group	Generation	Number of litter 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
B	0012	–	wc	3	3	2	2	2	2	2	3	3	3	2	1	3A							
F	0045	B	F1	3	1	3	1	A	A	4	3	3	4	3	A								
G	0032	B	F1	3	3	3																	
J	0060	B	F1	3	2	1	4	3	3	4	2	2											
K	0059	B	F1	3	?A	2	3	3	2	3	2												
L	0054	B	F1	3	3	3	4	3	2														
N	0053	B	F1	2	3	1	4	3															
V	0123	N	F2	2	3	3	2	2															
X	0245	K	F2	3	3																		
Z	0215	K	F2	2													Clan B						
C''	0231	K	F2	2	2																		
CC	0143	L	F2	3	3	3	3	A															
CF	0341	CF	F2	1																			
U	0257	J	F2	3																			
CD	0269	V	F3	1A	2	3	3	2	2	2	2	3	3	3	1								
CG	0270	V	F3	A	3	1																	
CH	0313	C''	F3	2	2	2	2	2	2	1	1A												
CS	0365	CD	F4	3	2	3																	
CT	0403	CD	F4	4																			
C	0011	–	wc	?A	2	2	2	2	1	3	3	3	3	1	3	3	2	3	3	2	2	3	1
I	0049	C	F1	3	3	3	2	3															
M	0051	C	F1	3	2	3	3	3															
R	0068	C	F1	3	3	3	2	3	3														
S	0038	C	F1	2	3	3	3																
C'	0052	C	F1	3	2	2A											Clan C						
M'	0136	M	F2	3	2																		
NN	0155	M	F2	2																			
CB	0166	R	F2	2	2	2	2	2															
CI	0251	C'	F2	2	3	3	1	3	3														
CM	0334	CB	F3	2	2	2	3	2															
CE	0302	–	F1	1	3	3	3	2	3	3	3	3											
CN	0383	CE	F2	3													Clan CE						
CU	0384	CE	F2	3	3																		
CL	0356	–	F1	2	2	3											Clan CL						
CR	0377	CL	F2	2	2																		
CJ	0349	–	F1	3	3	3	3	4	4	3	2												
CV	0410	CJ	F2	4													Clan CJ						

wc = wildcaught; A = abortion; 1 = singleton; 2 = twins; 3 = triplets; 4 = quadruplets; ? = litter size not identifiable.

rather great fluctuation of litter size occurred, which as a whole was shown by a decrease of Trs in favor of Sis and Tws.

The increase in parity of the F_3-females (n=4, 26 litters) are characterized by a further decrease of the frequency of Tr-births, however, not continuously, and by an increase of Tws.

A comparison of the litter with increasing parity of the consanguineous breeding females of our colony does not indicate a continuous increase in the number of Tr-deliveries, but shows a great fluctuation along the total sequence of births.

Captive born females of *C. jacchus* show a higher frequency of Trs in the first litter onwards, than do wc-females, but there is no further increase in the incidence of Trs during their individual lives.

The analysis of the question whether females which were born as a Tr would also give birth predominantly to Trs of Qus gave the following results. With 32 females of our colony we know the size of the litter in which they were born: 15 in Tr-, 14 in Tw-sets and 3 were singletons. 11 of the 15 Tr-females (=73.33 %) predominantly had Trs as well, whereas the rest (=26.67 %) did not correspond in this respect. In the females born in Tw-sets we could not find a tendency to give birth to Tws, they had just as many Tws as Trs (=42.86 % each). The singleton-females also, did not show any correspondance between the size of their litters and the fact they were singletons.

Discussion

The analysis of litter size of our *C. jacchus* females has shown, that as a whole the incidence of Tr-litters is slightly higher than that of Tw-births (see however Grist 1973; Hearn et al. 1975; Phillips 1976; Hiddleston 1977; Hampton et al. 1978; Ogden et al. 1978; McIntosh and Looker 1982). When one observes the litter size incidence as an annual event, as has been done in the literature, one sees a relative increase in number of the Tr- and Qu-deliveries and a decrease in the number of Tw-sets (Hiddleston 1976; Poole and Evans 1982; Burt and Plant 1983). This pattern was also observed in our colony (see Fig.). A more precise investigation, however, illuminated the fact that such a global

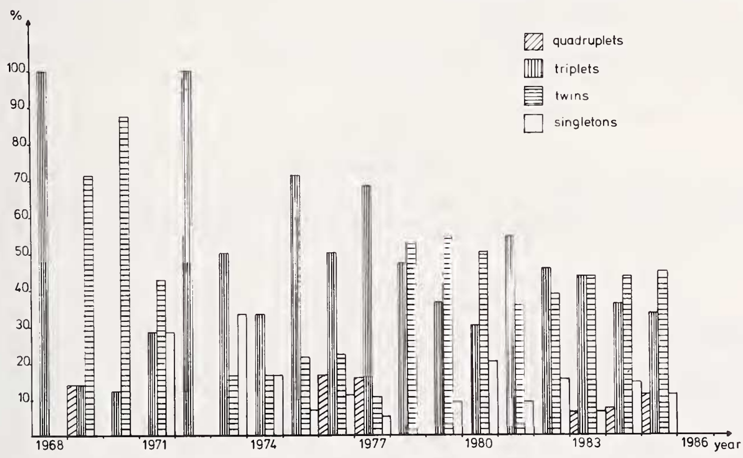

Fig. Annual variation of litter size in a colony of common marmosets

investigation, masks important details of litter size distribution. The eight wc-females of our colony gave birth to nearly twice as many Tws than Trs, and, moreover, we could not recognize a tendency to produce more Trs in conjunction with increasing length of captivity in our laboratory. On the contrary, they had a rather balanced frequency of Tr- and Tw-sets. The most conspicuous changes in the relative frequencies of Tr-/Qu- and Tw-/Si-deliveries compared to wc-females occurred in the F_1-generation, that is, in the daughters of the wc-females. The relative frequency of Qus increased by more than 300 %, that of Trs by more than 100 % whereas the frequency of Tws decreased by 150 %, and that of the Sis by about 50 % (Table 3). However in the following generations, F_2 to F_4, we could detect major differences in litter size distribution compared to that in the F_1-

generation, with a tendency to produce more Tws than Trs, than that already observed in the wc-females. This means, that in comparison to F_1-females we had observed a definite increase in Tw-, with an associated decrease in Tr-sets. A comparable result was described by PHILLIPS (1976), although the author did not make it quite clear wheather the "parents" were wild-caught or captive born. In his colony Tw-sets predominated (66.67 %, 159 litters).

The often repeated statement, that a refined management (e.g. HIDDLESTON 1978) will lead to an increase of Tr-deliveries, apparently is neither sufficient nor correct. Then, this would mean that the wc-females must have the greatest increase of Qu-/Tr-deliveries, due to some kind of "flushing effect"; however, this is most probably not the case. Even if there is increased ovulation rate due to better nutrition, medical care etc., the implantation rate would not be increased nor would the prenatal death rate/resorption rate of ova and/or zygotes be affected. This result as well as the observation that a once reached level in the frequency of Tr-sets will not be further increased in the course of a female's individual life, corresponds with results from the breeding of domestic animals. In domestic animals it has been found that a permanent and substantial supply of food has no positive effect on litter size, even the contrary may be the case, but an abrupt change, from a spare to an optimal feeding results in the phenomenon known as "flushing" – an increase in the number of ova being released (see for example KIRKWOOD 1983 for *S. oe. oedipus*). The enormous increase of Trs in the first litters of the group of F_1-females may in fact be a consequence of better colony management including a reduction of any stress-producing factors, or it may even be due to better adaptation to life under laboratory condition. At least the distribution of the Qus does not exclude the assumption that litter size has a management independent familiar disposition, but the change of the relative frequencies of Tr- and Tw-deliveries in the following generations, however, cannot be explained at the moment. The data of other *C. jacchus* colonies should also be analysed under this aspect in order to ascertain the true relationship between litter size and other factors.

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Zusammenfassung

Analyse der Wurfgröße in einer Kolonie von Weißbüscheläffchen (Callithrix jacchus)

202 Würfe von 44 züchtenden Weibchen des Weißbüscheläffchens wurden analysiert. Acht Weibchen waren Wildfänge, 15 gehörten der F_1-, 15 der F_2-, vier der F_3- und zwei der F_4-Generation an. 46,04 % (n=93) aller Würfe, deren Größe zweifelsfrei festgestellt werden konnte, waren Drillinge, 39,6 % (n=80) Zwillinge, 8,94 % (n=18) Einlinge und 5,45 % (n= 13) Vierlinge. Wildfangweibchen hatten weniger Drillinge (30,19 %) als Zwillinge (56,60 %). Bei den F_1-Weibchen stieg der Anteil der Drillinge auf 61,45 %, während Zwillingsgeburten klar in der Minderheit waren (21,69 %). F_2-Weibchen hatten nur 47,22 % Drillinge und 44,44 % Zwillinge. In der F_1-Generation sank die Häufigkeit der Drillingsgeburten auf 26,9 % und der Anteil der Zwillingsgeburten stieg auf 56,69 %. Bei den F_4-Weibchen gab es bis jetzt nur vier Geburten von zwei Weibchen, so daß wir über die Verteilung der Wurfgröße in dieser Generation noch nichts sagen können. Nach ihrer Wurfgröße unterscheiden sich Mutter und Töchter stärker als die Mutter und all ihre züchtenden weiblichen Nachkommen zusammen. Aus Drillingsgeburten stammende Weibchen warfen hauptsächlich Drillinge, während wir bei Weibchen aus Zwillingswürfen keine Neigung zu Zwillingsgeburten feststellen konnten. Sie hatten ebensoviele Zwillinge wie Drillinge (je 42,86 %).

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